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Signature of ocean warming in global fisheries catch

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Marine fishes and invertebrates respond to ocean warming through distribution shifts, generally to higher latitudes and deeper waters. Consequently, fisheries should be affected by 'tropicalization' of catch[1–4] (increasing dominance of warm-water species). However, a signature of such climate-change effects on global fisheries catch has so far not been detected. Here we report such an index, the mean temperature of the catch (MTC), that is calculated from the average inferred temperature preference of exploited species weighted by their annual catch. Our results show that, after accounting for the effects of fishing and large-scale oceanographic variability, global MTC increased at a rate of 0.19 degrees Celsius per decade between 1970 and 2006, and non-tropical MTC increased at a rate of 0.23 degrees Celsius per decade. In tropical areas, MTC increased initially because of the reduction in the proportion of subtropical species catches, but subsequently stabilized as scope for further tropicalization of communities became limited. Changes in MTC in 52 large marine ecosystems, covering the majority of the world's coastal and shelf areas, are significantly and positively related to regional changes in sea surface temperature[5]. This study shows that ocean warming has already affected global fisheries in the past four decades, highlighting the immediate need to develop adaptation plans to minimize the effect of such warming on the economy and food security of coastal communities, particularly in tropical regions[6,7].

Assessing the effects of climate change on marine fisheries is one of the challenges for sustainable management of marine ecosystems. Marine biota respond to ocean warming through changes in distributions and abundance[3,4,8], phenology[9] and body size[10], leading to alteration of community structure[4,8] and trophic interactions[11], and ultimately affecting fisheries[7]. Studies assessing the potential effects of climate change on global fisheries under scenarios of greenhouse gas emissions predict a large-scale redistribution of maximum fisheries catch potential[12,13] and increased vulnerability of many coastal fisheries to climate change, particularly in the tropics[6]. Climate change effects on some fisheries have been detected[14,15]. For example, the rapid increase in catches of red mullet (*Mullus barbatus*), a warm-water species, around the UK is suggested to be related to ocean warming[15]. However, a signature of the effect of climate change on global fisheries has so far not been demonstrated. Because marine fisheries contribute to the economy and food security of many coastal communities, fisheries' responses to climate change need to be better understood to inform the development of effective management and adaptation policies[7].

Shifts in distributions of exploited stocks are expected to affect their availability to fisheries. Spatial distributions of marine fishes and invertebrates are strongly dependent on the relationship between physiological optima and limits under different temperatures, oxygen levels and other biotic and abiotic conditions[16,17]. Organisms living in temperatures outside their thermal optima experience reduced aerobic scope, negatively affecting their growth and reproduction, and ultimately reducing their abundance[18]. In contrast, some species may find that areas previously unsuitable for their survival have become more favourable. Consequently, the distribution margins and centroids of many marine fishes and invertebrates shift following changes in ocean conditions[16], with a tropicalization of species compositions occurring as the ocean warms[1]. Concomitantly, species with limited dispersal potential or a narrow range of temperature tolerance, such as in semi-enclosed seas and tropics, will decrease in overall abundance[18,19].

We represent the temperature preference of species in fisheries catch by an index called mean temperature of the catch (MTC) (Fig. 1). This global index builds on previous use of temperature preferences to evaluate potential effects of climate change on fisheries locally[14,20]. We propose that ocean warming leads to increased catches of warmer-water species and decreased catches of colder-water species, resulting in an

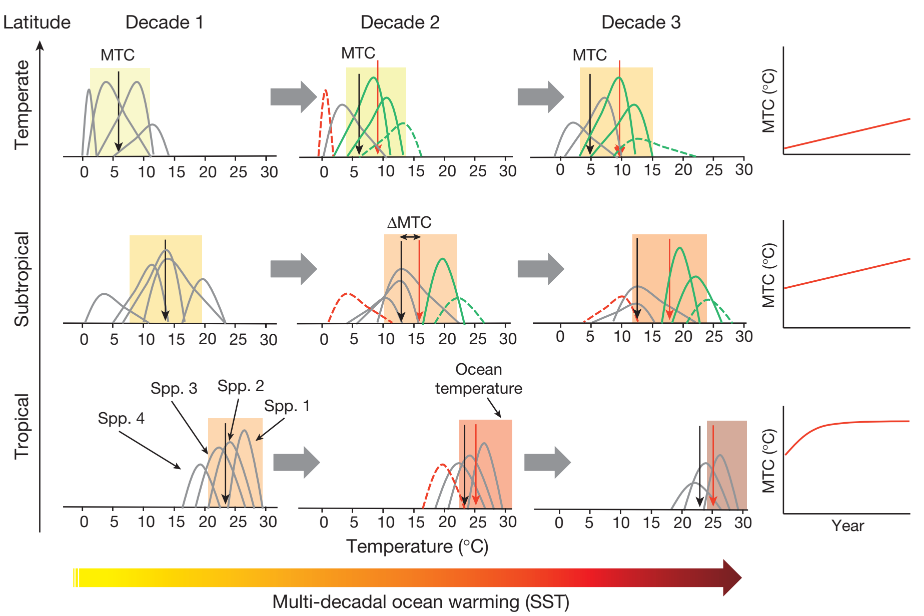

Figure 1 | Changes in catch species composition in relation to ocean warming and the resulting changes in MTC. Species distributions are related to ocean temperature (coloured bars) and temperature preferences of the exploited species (grey curves). Increase and decrease in abundance due to ocean warming are indicated by green curves and the reduction in area under the grey curves, respectively. The vertical black and red arrows represent MTC in the initial and subsequent decades, respectively. ΔMTC represents the difference in MTC relative to the initial decade. Species local extinction and invasion because of warming are indicated by red and green dotted curves, respectively. The expected changes in MTC over time are shown on the right.

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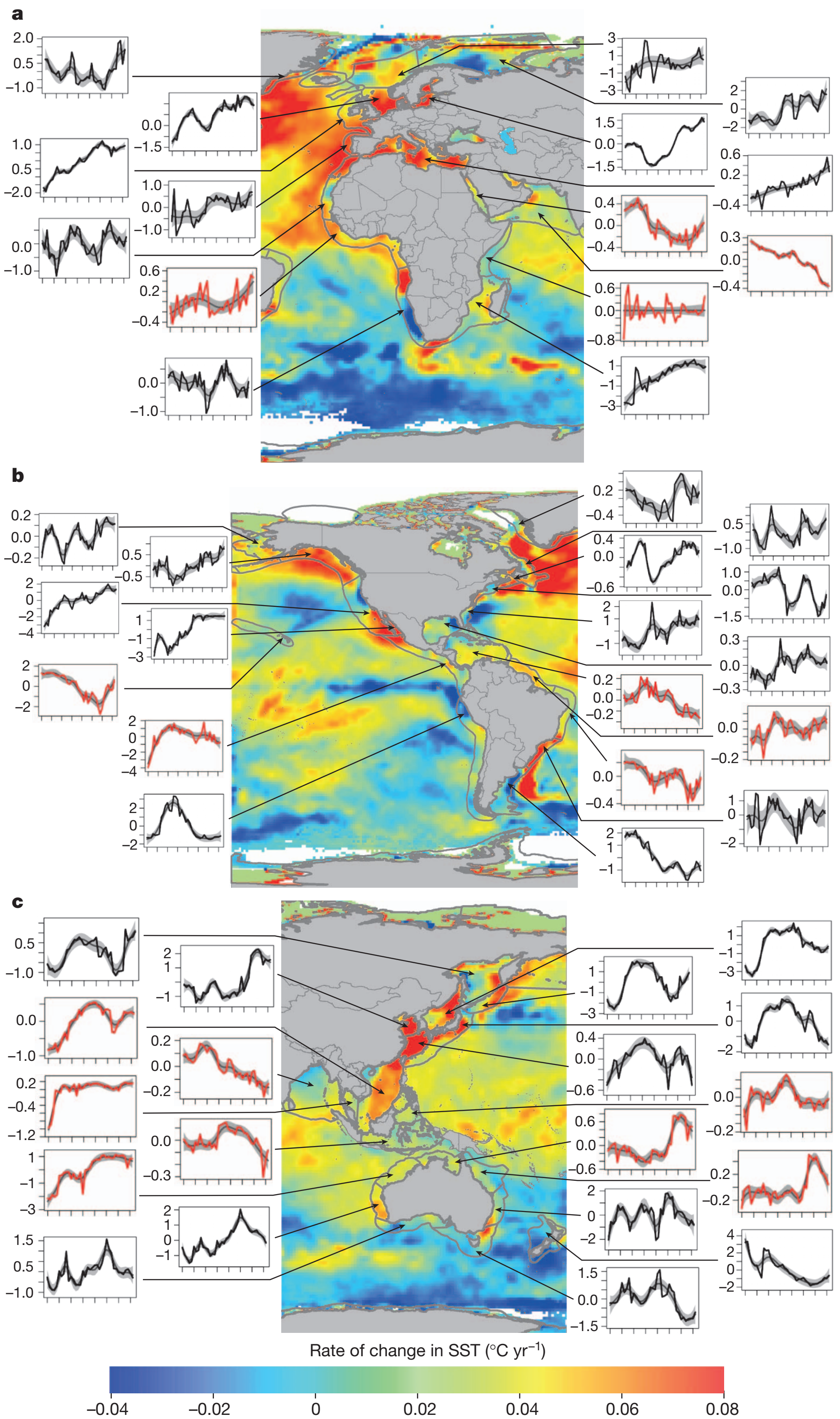

Figure 2 | Changes in MTC and SST of 52 LMEs between 1970 and 2006. Change over time (*x* axis; years between 1970 and 2006) in MTC anomalies relative to the mean of the time series (*y* axis; °C). Rate of SST change is shown by the colour scale. **a**, Eurasia; **b**, the Americas; **c**, Asia and Oceania. Red lines represent tropical LMEs. To highlight the nonlinear trends of MTC anomalies in this figure, each MTC time series was fitted with a spline smoothing function using GAMM: grey line, mean; shaded area, 95% confidence interval.

increase in MTC. We further propose that the general relationship between MTC and sea surface temperature (SST) is modified in the tropics, where catch compositions consist of both tropical and subtropical species. Warming would cause the initial decrease in the proportion of catches of subtropical species, resulting in increases in MTC because of the poleward shift in the equatorial range boundary of subtropical species. Such initial increases in MTC would then stabilize as catches become dominated by tropical species, but the scope for further tropicalization is limited[16]. Further warming, to levels that exceed the temperature preference and tolerance of tropical species, is then expected to reduce their abundance[12] without changes in MTC.

We calculated MTC as the average of the inferred temperature preference of exploited species (990 species in total) weighted by their annual catch between 1970 and 2006, for 52 large marine ecosystems (LMEs) that account for most of the world's fisheries (Methods). To attribute changes in MTC to ocean warming, we used a generalized additive mixed model (GAMM) with an ensemble of different combinations of factors to account for the potential effects of large-scale

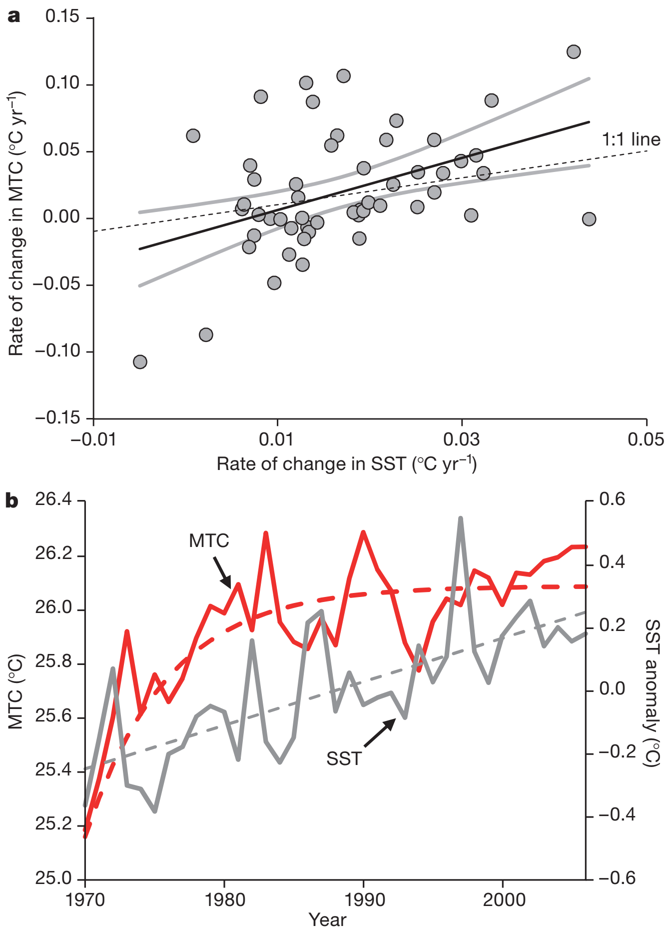

Figure 3 | Relationship between rates of change in MTC and SST between 1970 and 2006 in 52 LMEs. a, Rate of change of MTC was calculated from the ensemble GAMM in each LME (slope of linear regression, $P < 0.005$, $R^2 = 0.19$ (coefficient of determination)). The black line shows the mean and the grey lines delineate the 95% confidence interval. **b**, Changes in MTC (red) and SST anomalies (grey) in tropical LMEs. The dashed lines are fitted with asymptotic and linear models for the MTC and SST anomalies, respectively.

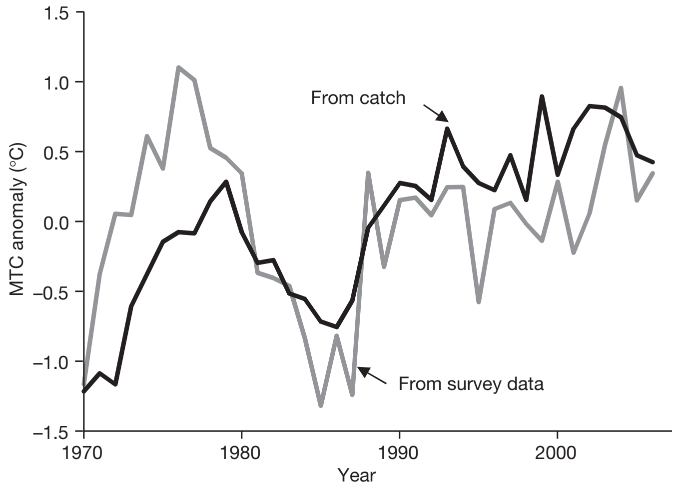

Figure 4 | Comparison of MTC calculated from fisheries catch data and relative abundance calculated from scientific survey data. MTC is expressed as an anomaly relative to the mean of the time series, and relative abundance is expressed relative to the average between 1970 and 2006. The type of data used had no effect on the rate of change in MTC (ANCOVA, $P > 0.1$).

oceanographic variability and fishing effort, both of which are known to affect fisheries strongly[21,22]. In addition, we repeated the analysis using a subset of 698 species with their temperature preference predicted from the above and an alternative approach to species distribution modelling (Supplementary Information).

Overall, the MTC in the 52 LMEs from the ensemble GAMM analysis increased at an average rate of 0.19 °C per decade between 1970 and 2006 (Fig. 2), and the MTC in non-tropical LMEs increased at a rate of 0.23 °C per decade. Specifically, MTC increased consistently in LMEs in the northeast Pacific Ocean (0.48 °C per decade) and the northeast Atlantic Ocean (0.49 °C per decade), where SST increased by 0.20 and 0.26 °C per decade, respectively. For each LME, and on the basis of the results from the ensemble GAMMs, we ranked the relative importance of SST, fishing effort and large-scale oceanographic indices as factors accounting for the changes in MTC over time. The results suggested that there was no significant difference between these factors, in terms of the frequency distribution of LMEs with different rankings (Kruskal–Wallis rank-sum test, $P > 0.05$; Supplementary Fig. 1). However, there were regional differences in their importance (Supplementary Table 1).

MTC changes in the 52 LMEs were significantly related to the rate of SST changes between 1970 and 2006 ($P < 0.05$; Fig. 3 and Supplementary Table 2). The relationships remained significant when the best models (lowest Akaike information criteria) were selected instead of the model ensemble (Supplementary Table 2) and when the twenty-fifth and seventy-fifth percentiles of the temperature preference profiles of the species, instead of the median values, were used in calculating the MTC (Supplementary Fig. 2). Using the alternative species distribution modelling approach to calculate species' temperature preference has no significant effect on the relationship between changes in MTC and SST ($P > 0.1$; Methods and Supplementary Information).

Tropical LMEs showed, overall, an asymptotic pattern of MTC change, with a reduction in the proportion of subtropical species in catches (Fig. 3). Average MTC from 14 tropical LMEs increased rapidly between 1970 and 1980 by around 0.6 °C, and subsequently stabilized at around 26 °C (Fig. 3). Moreover, the average temperature tolerance range, calculated from the difference in temperature between the twenty-fifth and seventy-fifth percentiles of the temperature preference profile of each species (Supplementary Information), decreased significantly during the period. Subtropical species had wider temperature tolerances than did tropical species[17] (Supplementary Fig. 3), providing further evidence to support the hypothesis that fisheries catches in the tropics are becoming inimical to subtropical species. Moreover, average SST change in the tropical LMEs increased consistently, at a rate of 0.14 °C per decade.

A number of factors indicate that MTC is a valid proxy to examine changes in composition of catches in a region in relation to the temperature preference of the exploited animals. First, there was no difference (analysis of covariance (ANCOVA), $P > 0.1$; Supplementary Table 4) between using catch data and scientific bottom trawl survey data in the calculated rate of change in MTC in North Sea (Fig. 4 and Methods). Because the scientific survey data set can be viewed as a reliable indicator of relative abundance of animals in the ocean, our results therefore support the use of catch data to detect climate change signature in fisheries. However, because the availability of survey-based data was limited to a few well-studied regions[23], we were unable to use such data to analyse global fisheries. The relationship between the thermal preference of the species and the environmental temperature also corroborates the results of regional-scale studies using survey data[14,24].

Second, fishing efforts in many LMEs have been increasing continuously since the 1970s. This coincided with increases in SST, resulting in strong correlation between changes in SST and fishing effort in some LMEs. However, there is no evidence that fishing systematically alters MTC. Specifically, significant but weak relationships between maximum body size (positively related to vulnerability to fishing, in general) and the temperature preference of exploited species is found in only 19 LMEs, with the majority (13) of them showing a positive relationship, suggesting that the increasing MTC trend was not a result of the depletion of large fish by fishing that was reported by many fisheries[25] (Supplementary Information).

Third, our findings are not an artefact of the quality of fisheries and environmental data, which vary between regions. In four of five areas in which misreporting of the level of catch was previously estimated, the estimated rates of change in MTC were not significantly different from those calculated from data sets without correction for misreporting. For the only area that showed a significant difference in rate of MTC change, MTCs calculated from both data sets show significant increase and the qualitative trend thus remains robust. Serious over-reporting of fisheries catches by China since the mid 1980s have been documented[26]. Recalculating MTC in the South China Sea, the East China Sea and the Yellow Sea using catch data from 1970–1985 increased the goodness of fit of its significant relationship with SST. The use of different SST climatology to calculate species' temperature preference, moreover, had no significant effect on the findings (Supplementary Table 3).

Although fisheries catch statistics are usually not reported at stock level, an analysis using simulated species and stock distributions, temperature preferences and, subsequently, MTC changes showed that the existence of stock structure and stock-specific temperature preferences did not significantly bias the rate of change of MTC calculated from aggregated species-level data ($P > 0.1$; Supplementary Information). Potential phenotypic and evolutionary responses of species to warming, if occurring, would reduce the rate of change in MTC. The accuracy of the SST data set varied between regions as a result of different densities of measurements. Given these uncertainties, the fact that our analysis is able to detect a signature of climate change in global fisheries highlights the robustness of the underlying relationship.

Overall, our results suggest that change in the composition of marine fisheries catch is significantly related to temperature change in the ocean, with an increasing dominance of catches of warmer waters species at higher latitudes and a decrease in the proportion of catches of subtropical species in the tropics. Such changes in catch composition have direct implications for coastal fishing communities, particularly those in tropical developing countries, which tend to be socioeconomically vulnerable to the effects of climate change[6]. Continued warming in the tropics to a level that exceeds the thermal tolerance of tropical species may largely reduce catch potential in this region[12]. This highlights the need to prioritize resources to develop adaptation plans immediately to minimize impacts on the economy and food security of tropical coastal communities.

METHODS SUMMARY

The mapped fisheries landings data were sourced from the Sea Around Us project[27], which utilized a range of sources including the Food and Agriculture Organization's (FAO) fisheries database supplemented by regional data sets (Supplementary Information). We inferred the thermal preference of each species on the basis of its modelled distribution[28,29] (Supplementary Table 5 and Supplementary Information). The MTC was computed from the average inferred temperature preference of 990 species of exploited fishes and invertebrates weighted by their annual catch:

$$\mathrm{MTC}_{\mathrm{yr}} = \frac{\sum_i^n T_i C_{i,\mathrm{yr}}}{\sum_i^n C_{i,\mathrm{yr}}} \quad (1)$$

Here $C_{i,\mathrm{yr}}$ is catch of species i in a specific region in year yr, T_i is the median temperature preference of species i and n is the total number of species. Similarly, MTC was calculated using survey data in the North Sea from equation (1) with $C_{i,\mathrm{yr}}$ replaced by the relative abundance for species i in year yr. Relative abundance data were obtained from the ICES International Bottom Trawl Survey. A total of 55 species common to both the catch database and the survey data set were included in this analysis. We tested the effect of the use of catch or survey data in estimating changes in MTC over time using ANCOVA, accounting for temporal autocorrelation.

We used the GAMM (R package MuMIn) with a full model, MTC = s(Effort) + s(OI) + Year, where s is a spline smoothing function (Supplementary Information) with a temporal autocorrelation term (R function corAR1), allowing for a lag of up to three years in the response of MTC to these two variables and the time effect expressed by Year. To estimate the average rate of change in MTC from the coefficients of this time effect, we did not include a spline smoothing function for Year. Fishing effort data were sourced from the Sea Around Us project[30] (Supplementary Information).

Full Methods and any associated references are available in the online version of the paper.

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Supplementary Information is available in the online version of the paper.

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Author Contributions W.W.L.C. and D.P. designed the study. W.W.L.C. conducted the analysis. R.W. and D.P. provided the fisheries catch and effort data from the Sea Around Us project. All authors contributed to the writing of the manuscript.

Author Information Reprints and permissions information is available at www.nature.com/reprints. The authors declare no competing financial interests. Readers are welcome to comment on the online version of the paper. Correspondence and requests for materials should be addressed to W.W.L.C. (w.cheung@fisheries.ubc.ca).

METHODS

Global catch and effort data. We use the terms fisheries catch and fisheries landings interchangeably, but strictly these both refer here to landings; the weight of marine fishes and invertebrates that were caught and retained. The mapped fisheries landings and effort data were sourced from the Sea Around Us project[27] (Supplementary Information). Landings data were not used to estimate temperature preference of the species, and temperature data were not used to infer species distributions. Effort data were standardized and collated on the basis of fishing boat engine power (watts) and fishing days[30] (Supplementary Information).

Inferring species' thermal preference. We inferred the thermal preference of each species from its modelled distribution (Supplementary Table 5). First, we modelled the present (1970–2000) distribution of each species using an algorithm developed by the Sea Around Us project and documented in ref. 28. The algorithm estimated the relative abundance (on a $30' \times 30'$ latitude–longitude grid) of a species in each spatial cell. Input parameters for each species considered in the model included the species' maximum and minimum depth limits, northern and southern latitudinal range limits, an index of association to major habitat types (seamounts, estuaries, inshore, offshore, continental shelf, continental slope and the abyssal) and known occurrence boundaries. For pelagic species, seasonal (summer and winter) distributions were considered. The parameter values of each species were derived from data in online databases, mainly FishBase (http://www.fishbase.org) and SeaLifeBase (http://www.sealifebase.org). Catch and temperature data were not used to model the current species distributions. Each modelled species distribution was normalized and overlaid over the SST climatology from the Hadley Centre SST data set for 1970–2000[29]. The predicted species distribution is considered to be representative of the distribution of relative abundance. The temperature preference profile at SST bin i (p_i) of each species was calculated from the total relative abundance, K_i, and range area, A_i, at SST bin i (Supplementary Information): $p_i = (K_i/A_i)/\sum_i(K_i/A_i)$.

The median and the twenty-fifth and seventy-fifth percentiles of the temperature preference were calculated. The modelled species distribution and temperature preference represents an average of the species' life stages. The analysis was repeated with alternative estimate climatologies for 1951–1960 and 1991–2000. The choice of climatology has no significant effect (ANCOVA, $P > 0.1$) on the relationship between rate of change in MTC and rate of change in SST (Supplementary Table 3). The analysis is also repeated using an alternative approach to species distribution modelling (Supplementary Information).

Calculation of MTC. The MTC was computed from the average inferred temperature preference of 990 species of exploited fishes and invertebrates weighted by their annual catch:

$$\mathrm{MTC}_{\mathrm{yr}} = \frac{\sum_i^n T_i C_{i,\mathrm{yr}}}{\sum_i^n C_{i,\mathrm{yr}}} \tag{1}$$

Here $C_{i,\mathrm{yr}}$ is catch of species i in a specific region in year yr, T_i is the median temperature preference of species i and n is the total number of species.

In the North Sea LME, MTC was calculated from equation (1) with $C_{i,\mathrm{yr}}$ replaced by the relative abundance for species i in year yr. Relative abundance data were obtained from the ICES International Bottom Trawl Survey. A total of 55 species that coexist in both the catch database and the survey data set were included in this analysis. We tested whether the changes in MTC calculated from catch data and scientific survey data were different, using ANCOVA and accounting for temporal autocorrelation.

Large-scale oceanographic indices. Indices representing large-scale oceanographic conditions for each of the six ocean basins were included in this study (Supplementary Information). For LMEs in the Pacific Ocean, their relationship with the Pacific decadal oscillation was used. For LMEs in the North Atlantic and South Atlantic, the North Atlantic oscillation index and, respectively, the dipole index were used. For LMEs in the Indian Ocean, the Indian Ocean dipole index was used. For LMEs in the Arctic, the summer sea-ice extent was used. For LMEs in the Southern Ocean, the Antarctic Oscillation index was used.

Accounting for the effects of fishing and large-scale oceanographic indices. For changes in MTC in each LME, we accounted for the effect of changes in total fishing effort (E) and the corresponding large-scale oceanographic index (OI). We then used a GAMM (R package MuMIn) with a full model, MTC $= s$(Effort $+ s$(OI) $+$ Year, where s represents a spline smoothing function (Supplementary Information), allowing for a lag of up to three years in the response of MTC to these two variables and the time effect Year, and including an autoregressive term to account for temporal autocorrelation. To estimate the average rate of change in MTC from the coefficients of the time effect, we did not include a spline smoothing function for the variable Year. These models were analysed using a multi-model analysis framework (R package MuMIn). There were significant autocorrelations of 1-yr lag in the MTC time series for all LMEs ($P < 0.05$). Rates of MTC changes (coefficient of Year) were estimated using a multi-model ensemble mean with weighting (W) calculated from $W_i = \exp[(\mathrm{AIC}_{\mathrm{min}} - \mathrm{AIC}_i)/2]$, where $\mathrm{AIC}_{\mathrm{min}}$ is the best model (that with minimum Akaike information criterion) and AIC_i was based on alternative model i. In addition, the rates of MTC change were also estimated from the model with the lowest Akaike information criterion. The relationship between the rates of change in MTC and SST remained significant with these alternative estimates.